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Cytogenetic and Fertility Studies of a Rheboon, Rhesus Macaque (*Macaca mulatta*) × Baboon (*Papio hamadryas*) Cross: Further Support for a Single Karyotype Nomenclature

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ABSTRACT Historically, two different numbering systems have been used to describe the baboon and macaque karyotypes. However, G-banding studies and, more recently, fluorescence in situ hybridization results have shown that the two karyotypes are virtually identical. To confirm this hypothesis, cytogenetic analysis of an unusual animal, a rheboon, was undertaken. The rheboon reported here, an 18-year-old male, is the only long-term survivor of 26 pregnancies resulting from matings between female baboons (*Papio hamadryas*) and male rhesus macaques (*Macaca mulatta*). A G-banded karyotype was prepared from the rheboon and compared with the karyotypes of the two parental species. Spectral karyotyping (SKY) was carried out on the rheboon chromosomes, and the results were compared with SKY studies reported for the baboon and with CISS (chromosome in situ suppression) studies in the rhesus macaque. No differences were detected in any of the rheboon's pairs of autosomes, reinforcing the apparent identity of the two parental karyotypes. Based on these results, we argue that a single karyotyping system should be adopted for the two species. Fertility studies were initiated to determine if the rheboon is sterile, as are most hybrid animals. Two semen ejaculates were devoid of sperm. A testicular biopsy revealed hypoplasia of the seminiferous tubules with few Leydig cells and large lumena. Meiotic arrest occurred during meiosis I, resulting in absence of mature spermatozoa. Thus, the testicular and meiotic findings in the rheboon were similar to those observed in other hybrids, even though the parental karyotypes appear identical. Am J Phys Anthropol 110:119–127, 1999.

Baboons (genus *Papio*) and macaques (genus *Macaca*) are among the most intensively studied of primate genera, and genetic analyses have been a significant part of this scientific attention. Unfortunately, the scientific literature describing the chromosomal structure and karyotypes of baboons and macaques is inconsistent and misleading. It is well established that baboons and macaques are closely related in phylogenetic terms, and are quite similar genetically (Disotell, 1994, 1996). Despite these similarities, the numbering systems used for chromosomes and karyotypes of baboons and macaques are different (see O'Brien et al., 1990;

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Graves et al., 1996). This nomenclature for these two karyotypes has a complex history, but the use of different systems stems mainly from a small number of studies, primarily prior to the development of chromosomal banding techniques, that suggested there are unique karyotypic features in each genus (e.g., Chiarelli, 1966). However, these studies contradict a larger number of studies of banded preparations that have found the karyotypes of baboons and macaques to be essentially identical (see Finaz et al., 1978; Pearson et al., 1979; Dutrillaux et al., 1979).

In order to resolve these discrepancies, we have examined the chromosomes and karyotype of an unusual animal: a hybrid between a male rhesus monkey and a female baboon. This animal's ancestry provides a unique opportunity to compare chromosome structure in baboons and macaques, and also presents opportunities for studies of reproductive function in primate intergeneric hybrids.

Chromosomal similarities among members of the subfamily Cercopithecinae, and between cercopithecines and humans have been recognized for many years (Chiarelli, 1966; Finaz et al., 1978). In 1979, the Committee on Comparative Mapping of the Human Gene Mapping 5 Workshop (HGM 5) used the information regarding chromosomal locations of functional genes, as well as the resemblance of chromosomal banding patterns between rhesus monkeys and humans, in preparing a standard karyotype for the rhesus macaque (Pearson et al., 1979). Previously, in the HGM 4 report (Pearson and Roderick, 1978), the committee had selected the karyotype of the rhesus monkey from a study by Stock and Hsu (1973) that utilized chromosome size, centromeric position, and the presence of a secondary constriction as the criteria for arrangement of the chromosomes. In the HGM 5 report (Pearson et al., 1979), the committee recognized that the chromosomes of *Macaca*, *Papio*, and other papionins were virtually identical. The report recommended that a common karyotypic representation be adopted for these genera and suggested that the karyotype arrangement developed for the rhesus macaque in the HGM 5 report could also be used for *Papio* and other papionins.

Later comparative mapping committees (see Roderick et al., 1984; O'Brien et al., 1990; Graves et al., 1996) returned to the historical karyotypes designated for each species. For baboons, they used an arrangement by Cambefort et al. (1976) based entirely on chromosome length, while the karyotype developed by the Comparative Mapping Committee in 1979, which was based on both chromosome length and homology to human chromosomes, was continued only for the rhesus macaque. This creates the impression that the genome structures of baboons and macaques differ greatly. For example, the gene for lactate dehydrogenase B (LDHB) is recorded as mapped to baboon chromosome 11 and to rhesus chromosome 12, although the banding patterns of these two chromosomes are identical. As primate genetic analyses turn to gene mapping and comparative gene localization, this discrepancy adds confusion and ambiguity to the literature.

Matings between macaques and baboons have been noted in the zoo literature for over a century (Markarjan et al., 1974; Kuehl and Harris, 1995). In the late 1970s, matings between female baboons (*Papio hamadryas*) and male rhesus monkeys (*Macaca mulatta*) were initiated at the Southwest Foundation for Biomedical Research (SFBR) in San Antonio, Texas to develop hybrid animals, which have been called rheboons. This work was done through an Institutional Animal Care and Use Committee-approved protocol, and was intended to evaluate the genetic regulation of serum cholesterol. The two species have greatly differing responses to dietary cholesterol, as baboons show a moderate response to diet, while rhesus monkeys demonstrate a much greater response (Carey, 1978).

METHODS AND MATERIALS

Study subject

Pregnancies were readily produced from matings between rhesus monkey males and baboon females. Twenty-six such pregnancies resulted from these matings, but spontaneous labor developed consistently about 5 weeks prematurely, at less than 154 days of gestation. The average length of gestation for baboons is 184 days and 165 days for

rhesus monkeys (Herring et al., 1991; Golub et al., 1988). Delivery in these hybrid pregnancies was by cesarean section when the females began premature labor.

Four infants survived the newborn period, two males and two females. Each of these four had a gestation greater than 145 days. The other 22 infants died within 72 hours due to complications of prematurity, primarily respiratory distress from hyaline membrane disease. This observation led to the development of an animal model for hyaline membrane disease that uses premature baboons. These premature infants are physiologically and pathologically similar to human premature infants (Kuehl and Harris, 1995; King et al., 1995; Morrow et al., 1995).

The animal studied here is the only long-term survivor of the rhesus macaque × baboon crosses. He is an 18-year-old male, weighing 15.42 kg, about the size of a female baboon (average weight at the Southwest Foundation for Biomedical Research [SFBR], 18 kg), but midway in weight between a baboon male (average weight at SFBR, 28 kg) and a rhesus macaque male (average weight at SFBR, 8 kg). His tail shape is more similar to that of a rhesus macaque, while his body shape and size are more similar to that of a baboon, except that his maxilla is foreshortened resulting in a significant underbite (Fig. 1).

A behavioral study of the rheboon reported that he exhibited unique behavior patterns (Kessel and Brent, 1997; L. Brent, personal communication). Some behaviors, such as mantle shake and eyebrow raise, were the same in form as those of the baboon. However, the rheboon was similar to the rhesus macaque in that he lacked the teeth grinding behavior of baboons. The rheboon did not display the open mouth threat behavior common to both the baboon and macaque. He displayed fewer vocalizations than either the baboon or macaque, and one vocalization appeared to be a combination of sounds similar to each parent species. The relative influence of genetic and environmental variables on the rheboon's behavior patterns is unknown. Although he has spent the majority of his life in single caging, the rheboon has had visual, olfactory, and tactile access to both baboons and rhesus macaques, thus providing behavioral learning opportunities from each species.

Fig. 1. Physical appearance of rheboon male at 18 years of age.

Cytogenetic studies

G-banded karyotypes were prepared from peripheral blood samples taken from the rheboon, a normal male rhesus macaque, and a normal male baboon. The samples were cultured in RPMI 1640 with 15% fetal bovine serum and concanavalin A as the mitogen. A standard blood culture and GTG-banding protocol were followed. Karyotypes were prepared and arranged according to Cambefort et al. (1976) for the baboon and rheboon and according to Pearson et al. (1979) for the macaque. A composite karyotype was prepared using both homologues from the rheboon cells, one homologue from the rhesus macaque preparation, and one from the baboon culture, following the arrangement of Cambefort et al. (1976)(Fig. 2).

Other slides from the rheboon were air-dried and prepared for spectral karyotyping

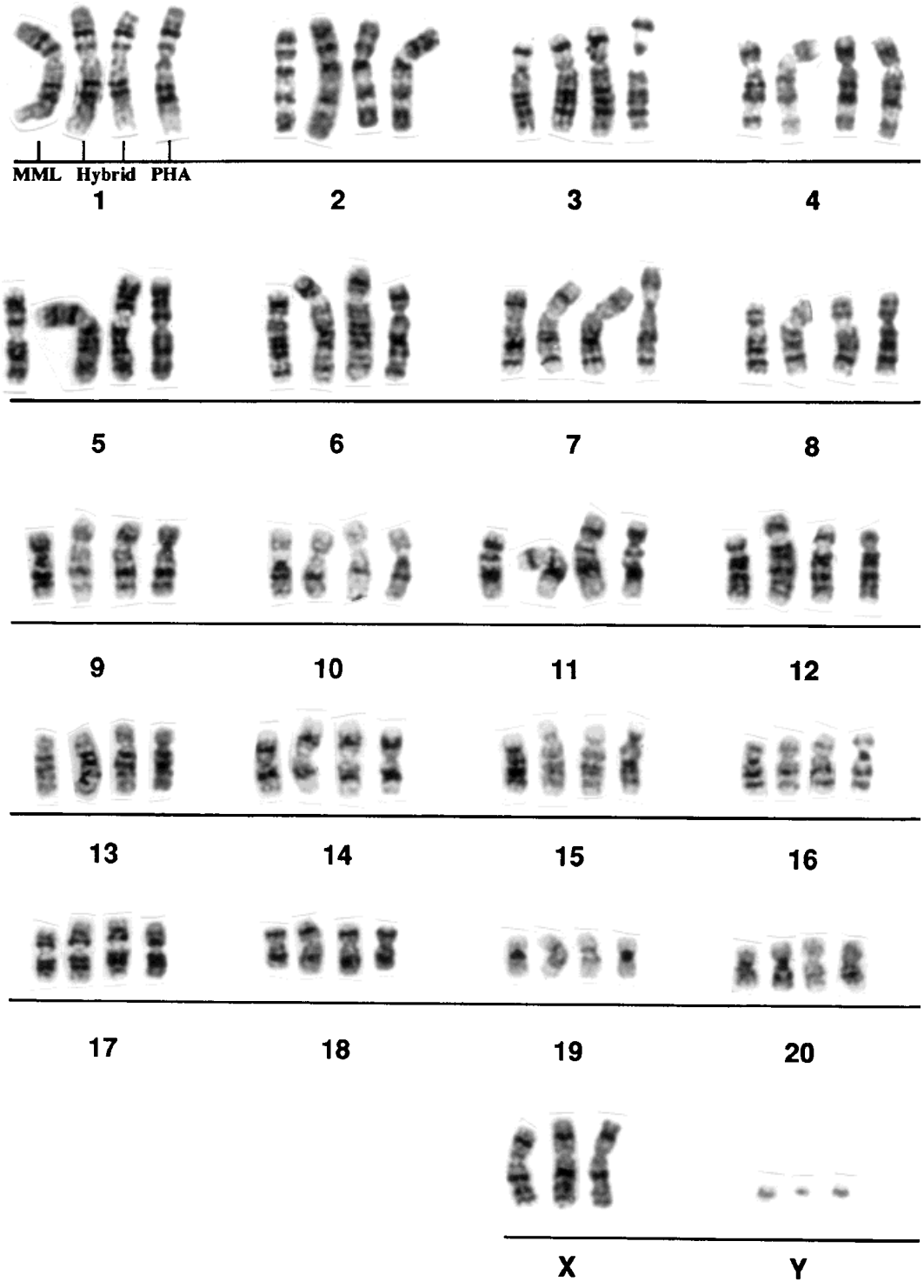


Fig. 2. Composite G-banded karyotype of the rheboon compared to homologous chromosomes from a baboon and a rhesus macaque arranged according to Cambefort (1976). The two homologues of the rheboon (Hybrid) are in the center of each set, while one homologous chromosome from the rhesus macaque (MML) is on the left and one from the baboon (PHA) is on the right.

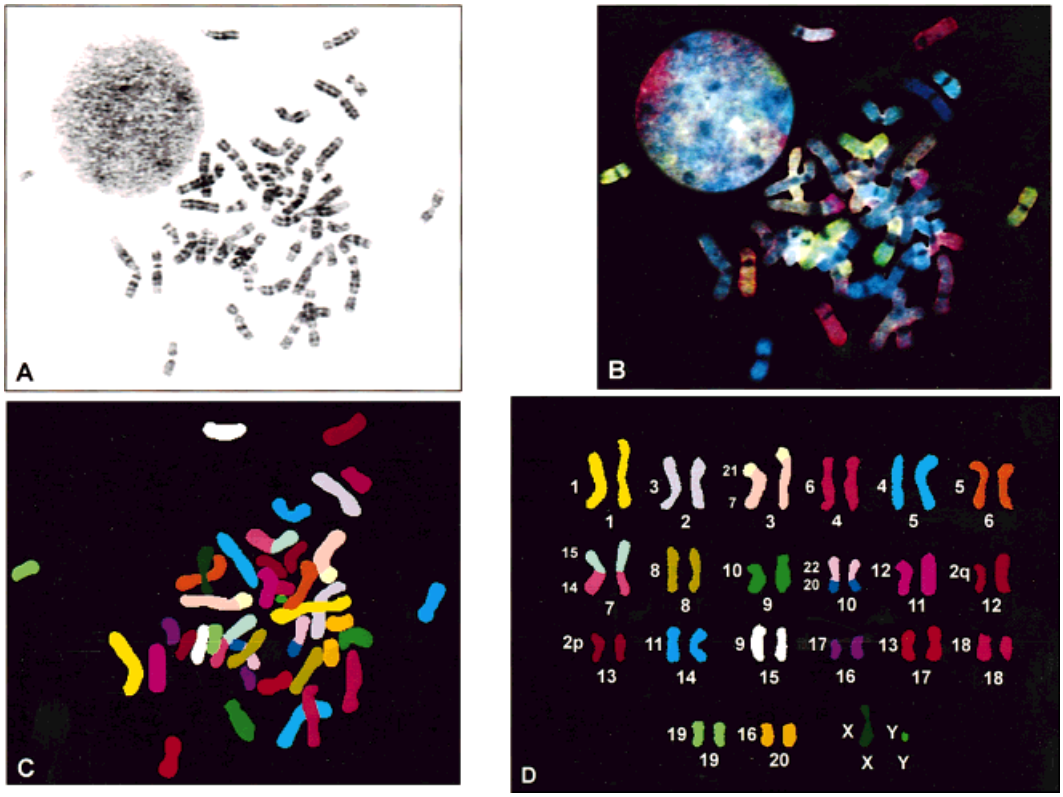
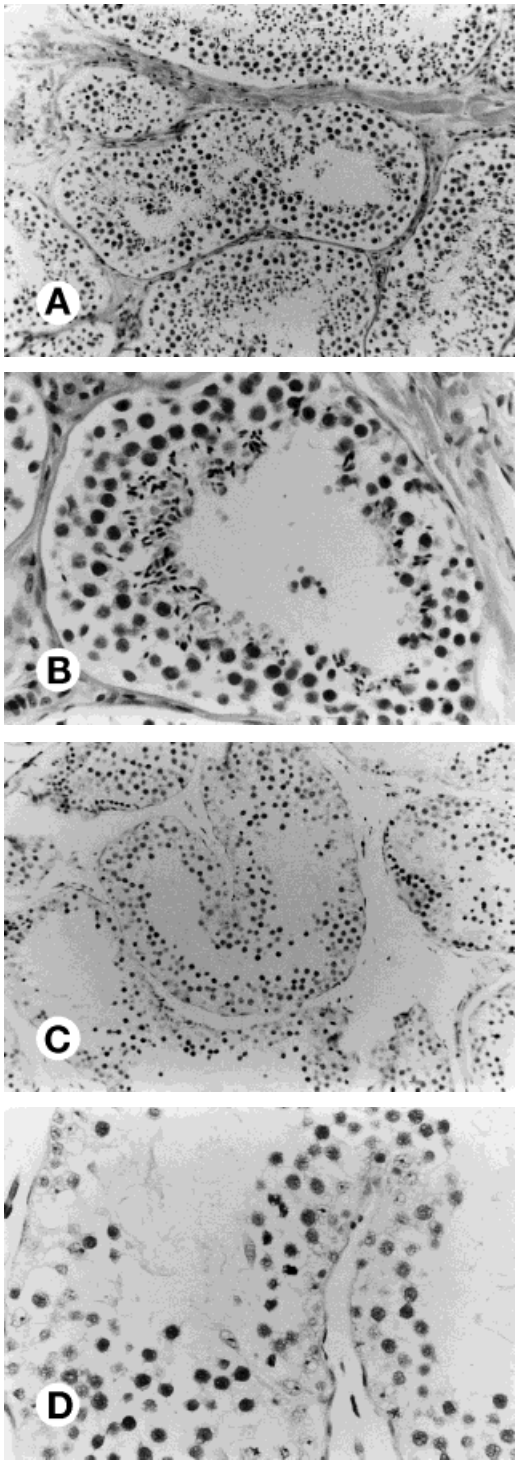


Fig. 3. **(A)** Metaphase from rheboon lymphocyte: DAPI inverted image. **(B)** Same metaphase: RGB display image. **(C)** Same metaphase: classified image. **(D)** Karyotype from classified SKY image arranged according to Cambefort (1976).

(SKY) following the Applied Spectral Imaging standard protocol (Best et al., 1998). Flow-sorted painting probes covering the entire length of all 24 human chromosomes were used. Each chromosome was uniquely identified with a combination of five directly incorporated labels (biotin, digoxigenin, Spectrum Green, Spectrum Orange, and Texas Red). Slides were counterstained using a DAPI/antifade solution. Fluorescent detection was achieved directly for Spectrum Green, Spectrum Orange, and Texas Red, and indirectly for biotin using an avidin-Cy5 conjugate. Digoxigenin detection was performed using a mouse anti-digoxigenin antibody followed by a goat anti-mouse antibody labeled with Cy5.5. SKY images were obtained using an SD200 SpectraCube™ spectral imaging system from Applied Spectral Imaging, Inc. (Carlsbad, CA). A corresponding DAPI image was also acquired and displayed as a pseudo-G-banding pattern for identification of individual chromosomes (Fig. 3A). The SKY system captured a unique spectrum at every image pixel after Fourier transformation. The raw spectral data were shown as a red-green-blue (RGB) display image by assigning the display color ranges to specific spectral emission ranges (R = near infrared emission, G = red emission, B = green emission) (Fig. 3B). A mathematical pixel classification was visualized as different pseudocolors (Fig. 3C). Karyotypes were prepared using the classified chromosome images (Fig. 3D).

Fertility studies

The fertility of the rheboon was investigated by examining two semen ejaculates produced by rectal probe electroejaculation. Semen evaluation was performed following appropriate dilution, using methods described for nonhuman primates (Kramer and Vera Cruz, 1989).



A testicular wedge biopsy was obtained while the animal was under anesthesia, prepared by fixation in 10% neutral buffered formalin, processed conventionally, cut into 5 μm sections and stained with hematoxylin and eosin (Fig. 4C and D). This was compared with a similar testicular biopsy from a normal fertile male baboon (Fig. 4A and B).

RESULTS

The rheboon karyotype was found to have a chromosome number of 42 chromosomes as expected. Each pair of homologous chromosomes is virtually identical in banding pattern. In the composite G-banded karyotype of the rheboon compared with homologous chromosomes of the baboon and rhesus macaque, each set of homologues is virtually identical, with the exception of the nucleolus organizing region (NOR) on chromosome 10 that shows normal variation in size. The parental origin cannot be distinguished for any of the individual rheboon autosomes; the origins of the rheboon X and Y were intuitive. This degree of similarity between the chromosomes of the baboon and rhesus macaque is consistent with the earlier results of identical G-banding studies (Finaz et al., 1978; Pearson et al., 1979), and argues against the use of two different systems of nomenclature.

Human chromosome painting probes hybridized strongly to the rheboon chromosomes across the entire genome with no detectable segments of nonhybridization. The karyotype generated by spectral karyotyping analysis is identical to the one obtained for baboons (Best et al., 1998) and is consistent with past inferences regarding chromosomal homology among primates (Anderson et al., 1996). Most of the rheboon chromosomes hybridized to probes derived from a single human chromosome. In three

Fig. 4. **(A)** and **(B)** Section from normal baboon testicular biopsy. A: Note germinal epithelium and supporting tissue (original magnification: 100×). B: Note presence of elongated, mature sperm near lumen (original magnification: 600×). **(C)** and **(D)** Comparable section from rheboon testicular biopsy. C: Note lack of supporting tissue with few Leydig cells and reduction in height of germinal epithelium with enlargement of the lumena (original magnification: 100×). D: Note absence of mature spermatozoa (original magnification: 600×).

cases, a single rheboon chromosome is homologous to two different human chromosomes. Rheboon chromosome 3 hybridizes with probes from human chromosomes 7 and 21, rheboon chromosome 7 with those from human chromosomes 14 and 15, and rheboon chromosome 10, the only chromosome with a nucleolus organizing region, with probes from human chromosomes 20 and 22. We note that these three rheboon chromosomes that have homologies to two human chromosomes all involve at least one human acrocentric chromosome sequence. Two rheboon chromosomes (12 and 13) showed homology to human chromosome 2. The latter has repeatedly been shown to result from a fusion of two separate chromosomes found in other primates (Estop et al., 1979; Paris Conference, 1975; Wienberg et al., 1992; Ried et al., 1993). As expected, chromosome 12 from the rheboon showed distinctive G-banding similarity to human 2q, and chromosome 13 was similar to human 2p.

The two semen samples obtained by rectal probe electroejaculation were devoid of sperm. The biopsy from the rheboon showed testicular hypoplasia (Fig. 4C and D) compared with that of a normal baboon (Fig. 4A and B). The hypoplasia was evidenced by abnormalities in the seminiferous tubules and supporting tissue. There was reduced height and amount of the germinal epithelium with few Leydig cells. The lumena of the seminiferous tubules were excessively large and were either empty or contain sloughed epithelium, proteinaceous debris, and nuclear fragments. Normal spermatogenesis was disrupted, with absence of mature spermatozoa. Apparently, meiosis was initiated because spermatogonia and primary spermatocytes were present, but fragmentation of the cells occurred at this point in development, instead of a normal progression to spermatozoa.

DISCUSSION

The karyotype of the rheboon presented here provides additional proof of the G-band identity of the rhesus and baboon karyotypes that has been recognized for many years (Finaz et al., 1978; Pearson et al., 1979; Stanyon et al., 1988). The SKY results are in agreement with those reported earlier by Wienberg et al. (1992) for the Japanese macaque (*Macaca fuscata*) and the rhesus monkey (*Macaca mulatta*) using chromosome in situ suppression (CISS) and with the SKY analysis performed by Best et al. (1998) on baboon (*Papio hamadryas*) chromosomes.

Best et al. (1998) compared the homologies established for the baboon, rhesus monkey, Japanese macaque, and human genomes based on gene mapping data or by banding patterns, CISS, and SKY results. The majority of the gene mapping data are consistent with the banding data; and, as suggested by Best et al. (1998), the few gene assignments that are not should be explored for confirmation or reinterpretation of the results.

With these exceptions, these results support the identity of the karyotypes of baboons and macaques. The Committee on Comparative Gene Mapping at the Human Genome Workshop 5 (Pearson et al., 1979) suggested that a single arrangement be accepted for the karyotypes of these species and presented a karyotype for the rhesus macaque that they recommended could also be used for karyotypes of *Papio* and other papionins. The rhesus karyotype that was developed was "a compromise between an ordination based entirely on chromosome length and arm ratio and placing chromosomes in their relative human position when there was general agreement on the homologies involved." However, this does not follow the standard convention recommended in the VIIIth International Congress of Primatology (Chiarelli and Corruccini, 1982), which was to use length as the only criterion for ordering the chromosomes. Soares et al. (1982), therefore, urged that future karyotype arrangements should be arranged according to international standards, i.e., by size and not by presumed homology to the human karyotype. The karyotype arrangement of Cambefort et al. (1976) for the baboon does follow this convention, using length as the single criterion for ordering the chromosomes. The data presented here are in accord with a single arrangement for both species, and following the recommendations of Chiarelli and Corruccini (1982) and

Soares et al. (1982), the Cambefort arrangement is the more appropriate one to use.

Markarjan et al. (1974) also described chromosomal studies of hybrids between macaques and baboons. However, these were of unbanded preparations, and exact pairing of homologues could not be assured. They found that all the viable births from these matings had 42 chromosomes and reported no major structural differences between the baboon and macaque members of chromosome pairs.

Markarjan et al. (1974) also reported a remarkable similarity of the physical appearance of the hybrid animals they studied to the phenotype of the animal reported here. In two offspring of a male *Macaca mulatta* × *M. nemestrina* species hybrid crossed with a female *Papio hamadryas*, they found, as we describe here, that the two female hybrids had a body build that resembled that of a baboon, but the form of the head, face and hair color was more like a macaque.

Other examples of intergeneric hybrids involving *Papio* have been described (see Hill, 1970 for a brief review). In a recent study, Jolly et al. (1997) analyzed several examples of hybridization between gelada baboons (*Theropithecus gelada*) and *Papio* baboons, which are sympatric in several regions of Ethiopia. They describe a captive colony that includes viable and fertile hybrids between *Papio* and *Theropithecus*. Because Jolly and his colleagues were able to investigate phenotypic variation within this group, as well as the pedigree of specific hybrid individuals, they were able to evaluate the inheritance of morphological features that distinguish these two species. Dunbar and Dunbar (1974) describe *Theropithecus-Papio* hybrids in the natural populations of the Bole Valley, Ethiopia. The fertility of the *Theropithecus-Papio* hybrids, despite the highly derived morphology of the geladas, contrasts with the demonstrated infertility of the rheboon. Given the chromosomal similarity of all three genera (Stanyon et al., 1988), it seems that fertility of papionin intergeneric hybrids is not necessarily related to karyotypic changes.

Although there are clear exceptions as in the *Theropithecus-Papio* hybrids described above, most interspecific hybrids have been infertile, or have had dramatically reduced fertility (Jones et al., 1997). The testes of these hybrid animals are often hypoplastic due to gametogenic arrest. However, the parental karyotypes have virtually always differed in chromosome number and banding patterns. It is remarkable, therefore, that in the rheboon, even though the karyotypes of the parental genomes were identical as was also the case in the gelada-*Papio* hybrids, the results of the rheboon testicular analyses were similar to those seen in the infertile hybrids. It will be enlightening, therefore, to carry out further studies to determine the amount of homologous pairing and recombination in this animal and the cause of spermatogenic arrest.

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